The Journal of Experimental Biology 209, 4091-4101
Published by The Company of Biologists 2006
doi:10.1242/jeb.02478

Foraging energetics of a nectar-feeding ant: metabolic expenditure as a function of food-source profitability

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Summary

We examined the quantitative relationship between the energetic costs and benefits of nectar collection by nectar-feeding ants, *Camponotus rufipes*. In the laboratory, individual workers were trained to visit an artificial feeder that provided a sucrose solution of 1%, 5%, 10%, 30% or 50% at controlled flows, in a similar span range to those observed in natural nectar sources. We measured foraging times, nectar loads collected, and CO_2 production during actual feeding, as an indication of the energy expenditure for a single forager. Results show an increase in individual metabolic rates with increasing flow rate of sugar solution, but no dependence on sucrose concentration. This increase in metabolic expenditure does not depend on the crop load attained while feeding, as intuitively expected, and is therefore a result of an increased activity brought about by the food-source profitability experienced by the forager. The energy gained during collection of sugar solution is always higher than the energy spent by the ant. Even with a food source of lower quality than a natural source, the ants gain ca. tenfold of what they spend. Based on a simplified model, we calculated that foragers of *C. rufipes* could travel from 0.5 to 9 km with the energy gained in a single foraging trip only. These results suggest that decreasing foraging time is more important than increasing individual energetic efficiency when workers of the nectar-feeding ant *C. rufipes* decide to stop drinking and return to the nest with partial crop loads.

Key words: *Camponotus rufipes*, central-place foragers, metabolic rate, nectar feeding.

Introduction

Insects are the most abundant and widespread of all terrestrial animals. Among them, ants are the most ecologically successful (Hölldobler and Wilson, 1990). A possible explanation is their social organization, which allows them to collectively exploit food sources, and to build complex nests that create a controlled environment for the inhabitants. The maintenance of a large colony is often associated with an efficient foraging strategy. The fitness of the colony is therefore directly related to its foraging success, i.e. the net energy obtained by the workers over their life span. Foraging performance can be constrained by many different factors including competition (Milinski, 1982), predation risk (Milinski and Heller, 1978; Nonacs and Dill, 1990), desiccation risk (Nonacs and Dill, 1990), forager's size (Medan and Josens, 2005), and food-source characteristics (Possingham, 1989; Schilman and Roces, 2003), and can be improved by other factors such as learning (Ganishaiah and Veena, 1988; Johnson, 1991; Veena and Ganeshaiah, 1991).

Ant workers are central-place foragers, i.e. they deliver collected food to a central location, the nest. The most common currencies used in economic analysis of foraging behavior are the rate of energy gain (net energy gain per unit time) and energetic efficiency (net energy gain per unit energy expenditure) (Krebs, 1981). Costs are measured as time and energy spent foraging. Most studies have evaluated time costs, which are easy to record, but only few investigations provide direct measurements of foraging costs. Depending on the food type being collected, gain–cost ratios in foraging ants range from 4 to 1000 for nectar-feeding and harvester ants, respectively (Fewell, 1988; Fewell et al., 1996).

Nectar-feeding ants repeatedly visit renewable resources such as extrafloral nectaries or aphid aggregations. Such renewable resources usually offer nectar at flow rates much lower than the maximal intake rate of individual ants. Therefore ants have to wait for the nectar to be produced. Rates of extrafloral nectar secretion are influenced by biotic and abiotic factors (Heil et al., 2000); however, these rates could be considered roughly constant for short periods of time. For instance, maximal rates of 0.12 μl min^{-1} per plant have been measured in species regularly visited by ants (Dreisig, 2000). When the maximal crop capacity of an ant worker is

considered, averaging 6–7 μl for workers of the ant, *Camponotus rufipes* (Schilman and Roces, 2003), it becomes clear that in order to fill its crop, workers of this species should spend about 60 min feeding.

Ants often leave a nectar source with only partially filled crops even under *ad libitum* conditions (Josens and Roces, 2000; Mailleux et al., 2000). The extent to which foragers fill their crop is a function of nectar concentration (Josens et al., 1998). In addition, we found that ants trained to collect sugar solution provided at various flow rates spent different times feeding, and returned to the nest with partial crop loads, depending on the nectar flow rate experienced at the source (Schilman and Roces, 2003). Under such conditions, it may be relevant for ants to adjust their foraging efforts at a patch in response to its quality, since both time and energy costs may depend on food-source profitability.

It is an open question whether the observed partial loading in *Camponotus*, with a concomitant reduction in feeding times, and therefore the early departure to the nest, results from a trade-off between maximizing loading and minimizing feeding and transport costs. Quantitative studies that manipulate nectar production rate in the natural range of nectar flows and calculate energetic gains and measure time and energy costs, are lacking.

Nectar-feeding ants catabolize carbohydrates to cover their energy demands. Thus, the analysis of their foraging performance is straightforward because gain and costs can be measured in the same units (amount of carbohydrates ingested or consumed per unit time). In the present study, we measured the metabolic rates of trained ants during undisturbed feeding, and investigated time and energy allocation during foraging as a function of the profitability of the visited food source, with profitability expressed either as the sugar concentration of the provided solution or its flow rate.

Materials and methods
Animals

A colony of *Camponotus rufipes* Fabricius consisting of one queen, approximately 600 workers and brood was used throughout the study. The founding queen was collected in November 1994 in Misiones, Argentina. The colony was reared in a plaster nest, kept in open-top Plexiglas containers (37 cm×57 cm×27 cm) with fluon-coated walls to prevent escape, and maintained at 25°C, 50% relative humidity and 12 h:12 h L:D regime (light-on: 07:30 h).

All measurements were performed while the colony had free access to *ad libitum* cockroaches and water but was deprived of sugar solution for 3–7 days. In this period, starvation does not significantly modify foraging behavior in this species (P.E.S. and F.R., unpublished data). For a detailed explanation of rearing conditions and standardization of the colony, see elsewhere (Schilman and Roces, 2005).

Food sources

Sucrose solutions of different concentrations were provided at various flow rates. All concentrations of fed solutions are reported as percentage sucrose equivalents (g solute per 100 g solution) (Sigma-Aldrich; Deisenhofen, Germany). A continuous and controlled flow rate of either 0.236, 1.18 or 2.36 μl min^{-1} sucrose solution, with concentrations of 1, 5, 10, 30 and 50%, were used. The flow rates assayed were provided by a nectar pump, and these rates span the natural range of extrafloral nectar secretion for plants regularly visited by ants. For instance, values ranging from 0.075 to 0.21 μl min^{-1} per plant were found for different plant species (Dreisig, 1988), and an average of 18.1% sugar (range: 6 to 34%) was reported for the natural nectar loads collected by the ant *Paraponera clavata* (Breed et al., 1987).

Respirometry measurements

The high-resolution respirometry system employed (Sable system TR-2, Sable System International, Las Vegas, NE, USA; resolution 0.01 p.p.m. CO_2) has been described elsewhere (Lighton, 1990). Briefly, CO_2- and H_2O-free air was drawn through an acrylic respirometric chamber (2.8 cm×2.8 cm×5.2 cm; volume=40.8 cm^3) at a flow rate of 300 ml min^{-1} STP controlled by a mass-flow controller. The CO_2 produced by the ant was measured by an IR-CO_2 analyzer (Li-Cor, Inc., Lincoln, NE, USA), and the data were stored in a computer. Each recording consisted of a variable number of data points taken at 1.5-s intervals. To determined CO_2 emission rates, the data acquisition and analysis system DATACAN V software was used (Sable System International, Las Vegas, NE, USA).

In all cases before and after each metabolic rate recording, the system baseline with the empty chamber was recorded. During analysis, the initial and final baselines were subtracted assuming a linear drift. All measurements were performed in a room with a controlled temperature of 25±0.5°C.

Experimental procedure

Each assay began by connecting the laboratory nest to a food patch by means of a 50 cm-long wooden bridge. Only a single worker was allowed onto the bridge and reach the respirometric chamber where the patch was placed (Fig. 1). Once inside the chamber, the CO_2 released by the ant was measured during 4 min prior to feeding, then during the actual feeding activity, and 4 min after feeding before the ant was allowed to leave the chamber. To do this, the ant was first allowed to enter into the chamber by itself, the chamber was then closed and the CO_2-release measured over 4 min prior feeding. After that time, the nectar pump, which provided nectar at a given flow rate, was switched on and the measurement continued during feeding. The feeding time of the individuals varied according to the concentrations and flow rates of the solutions offered, as previously reported (Schilman and Roces, 2003). When the ant voluntarily finished feeding and decided to return to the nest, the pump was switched off and the CO_2-release was measured for another 4 min post-feeding. Afterward, the chamber door was opened and the wooden bridge connected again in order to allow the ant to return to its nest. Workers immediately returned to the nest without trying to return to the respirometric
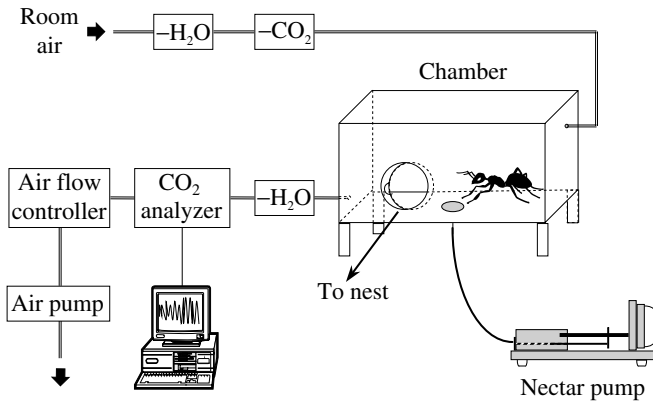
Fig. 1. Experimental design used to measure the metabolic rates of worker ants while foraging. Briefly, H_2O- and CO_2-free air was drawn through the respirometric chamber at a flow rate of 300 ml min^{-1} STP. The CO_2 produced by the ant was measured by an IR CO_2 analyzer and the data were stored in the computer.

chamber in order to collect more nectar. This was a clear indication that they voluntarily decided to stop feeding and return to the nest even with partial loads, as previously described (Schilman and Roces, 2003). For future identification, the worker was gently marked with colored powder when running back over the bridge. Upon arrival at the nest, the marked worker was allowed to enter and to unload the collected fluid *via* trophallaxis with nestmates. After unloading, the marked worker returned to the patch. Each marked ant performed 4 consecutive visits to the artificial food source inside the chamber, collecting nectar during all of them. The ant's metabolic rate was measured in the first and fourth visit. In the second and third feeding visits, the marked ant was allowed to enter an identical chamber that was not connected to the respirometric device. This allowed us to measure the baselines of the empty respirometric chamber used, while the ant was foraging in the alternative chamber, and so to control for any kind of electronic drift of the device. When the marked ant attempted the fifth visit, it was caged before entering the chamber so as to measure its unloaded body mass to the nearest 0.01 mg (analytical balance Ohaus Model AS60, Karlsruhe, Germany). The experimental procedure for measuring a single ant was time consuming, but ensured a record of non-disturbed feeding and metabolic expenditure of foraging ants.

A potential methodological artefact that might compromise our measurements could be the release of CO_2 dissolved in the nectar delivered by the pump. In order to control for that possibility, measurements with an empty chamber were performed in the same way as described above, but with no ant present in the chamber. Briefly, CO_2 was measured for 4 min with the nectar pump turned off, then for 30.52±0.24 min (for the flow rate 0.236 μl min^{-1}; mean ± s.e.m.), 10.50±0.13 min (for 1.18 μl min^{-1}) and for 5.41±0.07 min (for 2.36 μl min^{-1}) with the pump turned on, and finally for another 4 min with the pump off. The measuring interval with the nectar pump on, represents the highest experimental feeding times measured,

which depend on both the solution flow rate and sucrose concentration. As a consequence, exactly the same experimental procedure was employed in these control measurements, but without the ant. These controls were performed with all experimental flow rates assayed, using a sucrose concentration of 30%. For each measurement, the difference between the average CO_2 production over the 4 min before and during nectar delivery was calculated. Differences between the averages were expressed as absolute values (in μl h^{-1}) and as percentages of the experimental groups, as follows:

$$\text{Control} = (DN - BN) \times 100 / EXP, \quad (1)$$

where DN is the average of the CO_2 production rate for the time of nectar delivery (pump on), BN is the average for the 4 min before the pump was turned on, and EXP is the average CO_2 emission of ants at the same experimental conditions (i.e. same sugar concentration and rate).

Measurements and calculations of 'instantaneous' metabolic rate

During feeding, workers' body mass increases because of the collected load, and it is an open question whether the extent of loading may cause changes in the average metabolic expenditure during a visit. In order to separate the effect of the carried load from the effect of the food source profitability on the metabolic rate, we calculated 'instantaneous' metabolic rates. We defined 'instantaneous' metabolic rate as the average metabolic rate over a very short time interval, within which the worker reached a defined crop load during its actual feeding event. Using these previously defined crop loads as independent variables, it was possible to compare the 'instantaneous' metabolic rates of workers having the same crop loads, but collecting at different flow rates or sucrose concentrations. Each ant's CO_2 production rate was calculated at the time when the crop load of the individuals reached either 1, 3, 5 or 7 mg of load during their feeding activity. These measurements were converted to energy units of μW. We calculated, for each ant and load, the 'instantaneous' metabolic rate as the averaged measurement within either 30, 45, 60, 90 or 120 s. Taking into account the 1.5-s interval sampling of the recordings, these intervals were the average of 20, 30, 40, 60 and 80 measuring points, respectively. To obtain reliable 'instantaneous' measurements, it is important to note that the shorter the time interval chosen, the more realistic the instantaneous measure should be because of a lower variation on loads associated with different flow rates and sugar concentration. On the other hand, the shorter the interval chosen, the higher the probability of errors produced by spontaneous fluctuations in CO_2 emission due to the cycled pattern of gas exchange. Thus, to choose the most appropriate time interval, we calculated the coefficient of variation (V) for each group, load and span time, as follows:

Coefficient of variation or coefficient of variability:

$$V = \text{s.d.} / X \times 100, \quad (2)$$

where V is the coefficient of variation, which is a relative

measure without units, s.d. the standard deviation and X the mean (Zar, 1984).

We found statistically significant differences of the V values using a one-way ANOVA ($F_{4,147}=2.450$, $P=0.049$). *A posteriori* Tukey analysis did not show significant differences. However, a less conservative *a posteriori* analysis (LSD) showed that the 30-s interval was significantly higher than the others (LSD, $P<0.05$), but no other significant differences were found among the others. The fact that we did not detect differences between 45, 60, 90 and 120 s with a test like LSD, which has a higher possibility of finding false differences than more conservative tests, suggests that there are no differences among those intervals. Thus, we finally chose the 45-s average because it was the shortest interval with the low V value without significant differences compared to the longer intervals, i.e. 60, 90 and 120 s.

Data analyses and statistics

Out of a total of 285 metabolic recordings, only those in which the ant completed the four visits to the feeder, i.e. 250 recordings made by 125 ants (first and fourth visits), were considered for further analysis. CO_2 emission rate was converted to energy units of μW, assuming (as is reasonable for carbohydrate-feeding ants) the dissipative catabolism of glucose. Data were analyzed by one- and two-way analysis of variance (ANOVA) as well as with linear regressions after logarithmic transformation when appropriate (Zar, 1984). Although the metabolism of two foraging visits was measured for each individual, the average of these two visits was used for statistical analysis in order to avoid pseudoreplication (Hurlbert, 1984), except for the regression between metabolic rate and final crop load where the two visits were analyzed separately. In all cases, values are given as mean ± s.e.m. A probability of error $P<0.05$ was considered statistically significant.

Although *C. rufipes* can be considered as a polymorphic species (Hölldobler and Wilson, 1990), we measured, to facilitate comparison of data, workers of similar medium size in all experiments.

Results

Metabolic rate as a function of sucrose concentration

Across experiments, we found no significant differences in ant body mass (ANOVA: $F_{9,115}=0.588$, NS). The average body mass of unladen workers was 14.79±0.35 mg (mean ± s.e.m.). This fact allowed the comparison of metabolic rates (in μW) among treatments without the need to calculate mass-specific metabolic rates.

An example of a respirometric record from a foraging ant collecting 30% sugar solution at a flow rate of 1.18 $\mu l\ min^{-1}$ is presented in Fig. 2. Three different parts can be recognized on the plot, i.e. before, during and after feeding. Before and after feeding, a clear discontinuous pattern of CO_2 production is evident, corresponding to the activity of the ant inside the chamber. The CO_2 emission turned out to be more regular
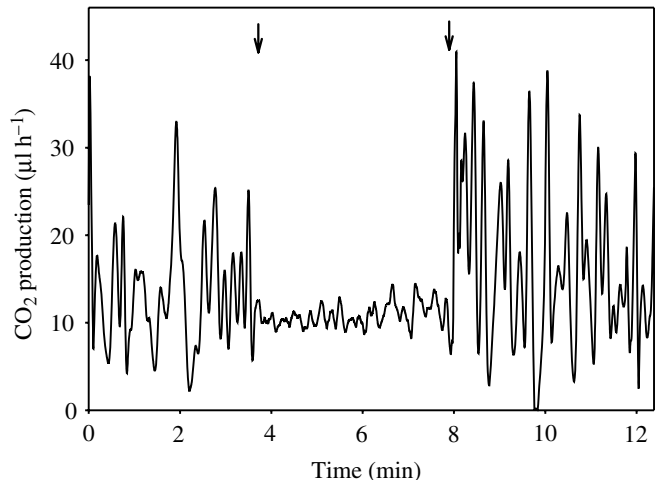

Fig. 2. Example of a respirometric record for a foraging ant at 1.18 $\mu l\ min^{-1}$ and 30% sugar concentration food source. CO_2 production rate (in $\mu l\ h^{-1}$) is plotted as a function of time. There are three different parts: (1) before drinking (ca. 4 min), (2) while the ant drinking at the feeder (between arrows) and (3) after feeding (also ca. 4 min).

during feeding. We compared CO_2 emission rates during actual feeding (Fig. 2, between arrows) among treatments.

To investigate the effect of sucrose concentration on metabolic expenditure while feeding, we presented individual ants in independent assays with 5 different concentrations of sugar solutions (1, 5, 10, 30 and 50%) at a constant flow rate of 1.18 $\mu l\ min^{-1}$. Feeding times increased with increasing sucrose concentration (Fig. 3A, one-way ANOVA, $F_{4,69}=6.348$, $P<0.001$). Since the sucrose solution was provided at the same flow rate, the longer feeding times resulted in larger crop loads with increasing sucrose concentration (Fig. 3B, one-way ANOVA, $F_{4,69}=11.673$, $P<0.001$). However, the variation of crop loads and feeding times with sucrose concentration are not exactly the same because loads were expressed in mass units (mg), and the density of a sucrose solution depends on its concentration (Wolf et al., 1984). Metabolic rate during feeding showed a tendency to increase with increasing sucrose concentration, although the differences were not significant (Fig. 3C, one-way ANOVA, $F_{4,69}=0.346$, NS).

Metabolic rate as a function of nectar flow rate

The profitability of a food source strongly depends on the amount of energy available per unit time. In Fig. 4, we analyzed the effect of the delivered flow rate on both feeding behavior and metabolic expenditure, for three different sucrose concentrations and flow rates. Fig. 4A shows a decrease of feeding time (min) with increasing nectar flow rate and sucrose concentration. Data for the series using 1% sucrose provided at 2.36 $\mu l\ min^{-1}$ are lacking. A solution of 1% sucrose was in general a poor stimulus for keeping the ant collecting the solution. This, together with the high flow rate used in this series (2.36 $\mu l\ min^{-1}$), resulted in a rapid accumulation of sugar solution at the feeder waiting to be ingested, which makes the
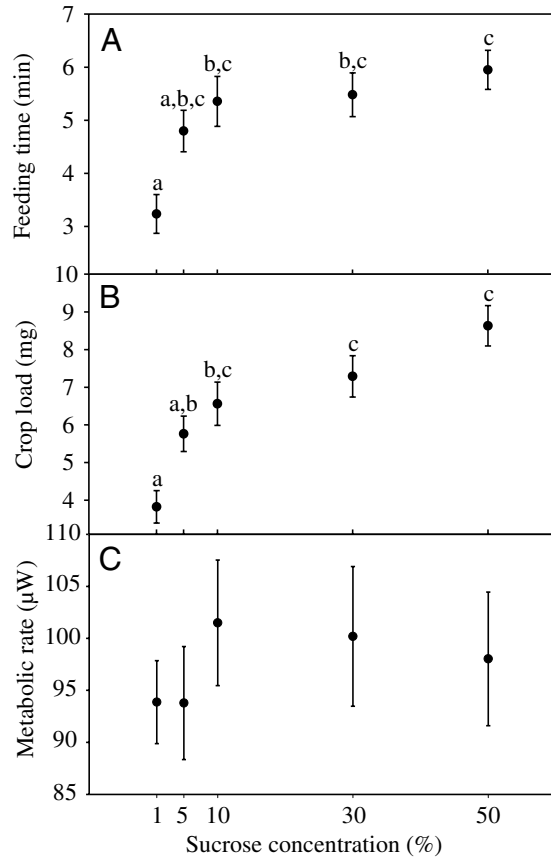
Fig. 3. Feeding time (min) (A), crop load (mg) (B) and metabolic rates of foraging ants (μW) (C) as a function of five different nectar concentrations (1, 5, 10, 30 and 50%) and a flow-rate of 1.18 μl min^{-1}. Values are means ± s.e.m. (N=13–17). *Posteriori* (Tukey test after one-way ANOVA): a,b, $P<0.01$; a,c and b,c, $P<0.001$; same letters do not differ significantly.
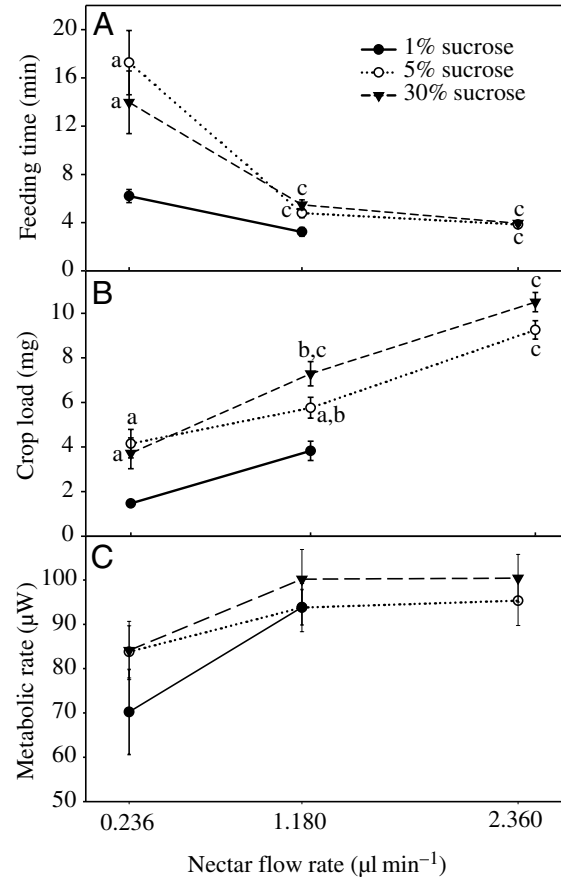

Fig. 4. Feeding time (min) (A), crop load (mg) (B), and metabolic rates of foraging ants (μW) (C) as a function of three different flow rates (0.236, 1.18 and 2.36 μl min^{-1}) and three different sugar solution concentrations (1, 5 and 30%). Values are means ± s.e.m. (N=6–17). *Posteriori* (Tukey test after first two-way ANOVA): a,b, $P<0.01$; a,c, $P<0.001$; same letters do not differ significantly. *Posteriori* (Tukey test after second two-way ANOVA: analysis differences between all concentration of 0.236 and 1.18 μl min^{-1}, i.e. we did not take into account the 2.36 μl min^{-1} groups): for (A) 0.236 μl min^{-1} and 1% *vs* 0.236 μl min^{-1} and 5% or 30% ($P<0.001$), 0.236 μl min^{-1} and 5% or 30% *vs* 1.18 μl min^{-1} and 1% ($P<0.001$); for (B) 0.236 μl min^{-1} and 1% *vs* 1.18 μl min^{-1} and 5% or 30% ($P<0.001$), 1.18 μl min^{-1} and 1% *vs* 1.18 μl min^{-1} and 30% ($P<0.001$); for (C) 0.236 μl min^{-1} and 1% *vs* 1.18 and 30% ($P<0.05$).

measurement of crop load not feasible. For the other, more attractive sucrose concentrations, no accumulation occurred, since the highest flow rate assayed lies well below the maximal intake rates of *Camponotus rufipes* (Schilman and Roces, 2003; Paul and Roces, 2003). Comparing 5 and 30% sucrose solution, feeding times significantly depended on flow rate ($F_{2,71}$=54.495, $P<0.001$), but not on sucrose concentration ($F_{1,71}$=0.816, NS). There was no interaction of both factors, i.e. flow rate and concentration ($F_{2,71}$=1.553, NS). In a second two-way ANOVA, we examined the differences among the three sucrose concentrations at 0.236 and 1.18 μl min^{-1}. We did not take into account the 2.36 μl min^{-1} groups for the reason mentioned above. Feeding time depended on flow rate ($F_{1,63}$=54.225, $P<0.001$) and concentration ($F_{2,63}$=11.678, $P<0.001$), and the interaction between flow rate and concentration was also significant ($F_{2,71}$=6.307, $P<0.005$).

Fig. 4B shows an increase of the crop load with increasing flow rates and sucrose concentrations. Comparing 5% and 30% for the three flow rates assayed, we found significant differences of crop load as a function of the nectar flow rate ($F_{2,71}$=56.985, $P<0.001$) but not with the nectar concentrations

($F_{1,71}$=3.164, NS); the interaction between flow rate and concentration was not significant ($F_{2,71}$=1.682, NS). In a second two-way ANOVA analysis of differences among all concentrations at 0.236 and 1.18 μl min^{-1} (we again did not take into account the 2.36 μl min^{-1} groups), we found highly significant differences of crop load as a function of the nectar flow rate ($F_{1,63}$=27.936, $P<0.001$) and concentration ($F_{2,63}$=12.047, $P<0.001$). The interaction between flow rate and concentration was not significant ($F_{2,71}$=1.605, NS).

Metabolic rate (μW) varied with increasing flow rate and sucrose concentration (Fig. 4C). Comparing 5 and 30% for the three flow rates assayed, we found no significant differences of metabolic rates as a function of the nectar flow rate ($F_{2,71}$=2.707,

NS) or as a function of sucrose concentration ($F_{1,71}$=0.571, NS); there was no significant interaction ($F_{2,71}$=0.107, NS). In a second two-way ANOVA analysis of all concentrations at 0.236 and 1.18 μl min^{-1}, we detected significant differences of metabolic rate with the nectar flow rate ($F_{1,63}$=9.505, P<0.005), but not with concentration ($F_{2,63}$=1.067, NS); the interaction term was not significant ($F_{2,71}$=0.539, NS).

Control measurements for 30% sugar solution gave the following variation in CO_2 between the first 4 min (prior to switch on the pump) and the nectar delivery time (during pump on): for 0.236 μl min^{-1}: –0.123±0.236 μl h^{-1} of CO_2 (mean ± s.e.m., N=7), which represents –0.86±1.65% of change with respect to the ant's measurements, for 1.18 μl min^{-1}: 0.321±0.092 μl h^{-1} of CO_2 (mean ± s.e.m., N=9) or 1.89±0.54%, and for 2.36 μl min^{-1}: 0.004±0.192 μl h^{-1} of CO_2 (mean ± s.e.m., N=9) or 0.03±1.12% of CO_2 emitted by an ant.

Metabolic rate as a function of increasing crop load during feeding

As mentioned above (Fig. 4), both crop loading and metabolic rate increased with increasing nectar flow rate. To determine whether the increase in metabolic rate is a direct consequence of the load carried, or whether the perceived nectar flow influences the ant's activity and thus its metabolic expenditure while feeding, irrespective of the crop load, we compared 'instantaneous' metabolic rates of animals at those times at which they reached similar crop loads.

Both Fig. 5 and Table 1 show the separate effects of the actual crop load and the nectar flow on the 'instantaneous' metabolic rates. Nectar flow had a large effect on metabolic rate when controlled for load (for instance, compare the values at rates of 0.236 and 2.36 μl min^{-1} for a load of 3 mg, Fig. 5). Another way to determine the relationship between metabolic rate and loading is through a linear regression of metabolic rate as a function of the final crop load at the end of the visit for each different experimental group and visit (i.e. first and fourth visits). If the magnitude of loading affects metabolic expenditure, a positive relationship between final crop load and metabolic rate should be expected. Table 2 shows the values of the regression for three different flow rates (0.236, 1.18 and 2.36 μl min^{-1}), five different concentrations (1, 5, 10, 30 and 50%) and two different visits (first and fourth). From the 20 different regressions performed only one was slightly significant (group 2.36 ml min^{-1}, 5%, fourth visit, P=0.039) with load explaining less than 35% of the metabolic rate (Table 2).

Gain, costs and foraging energetics

Fig. 6 shows the relationship between the energy spent, directly measured *via* respirometry, and the energy gain, which was contained in the nectar collected by the individual ant, for the different flow rates and sucrose concentrations assayed. Energy gain was always higher than the energy spent by the ant, even for the poorest profitability offered, i.e. 0.236 μl min^{-1} and 1%. Even for the poorest food source, the
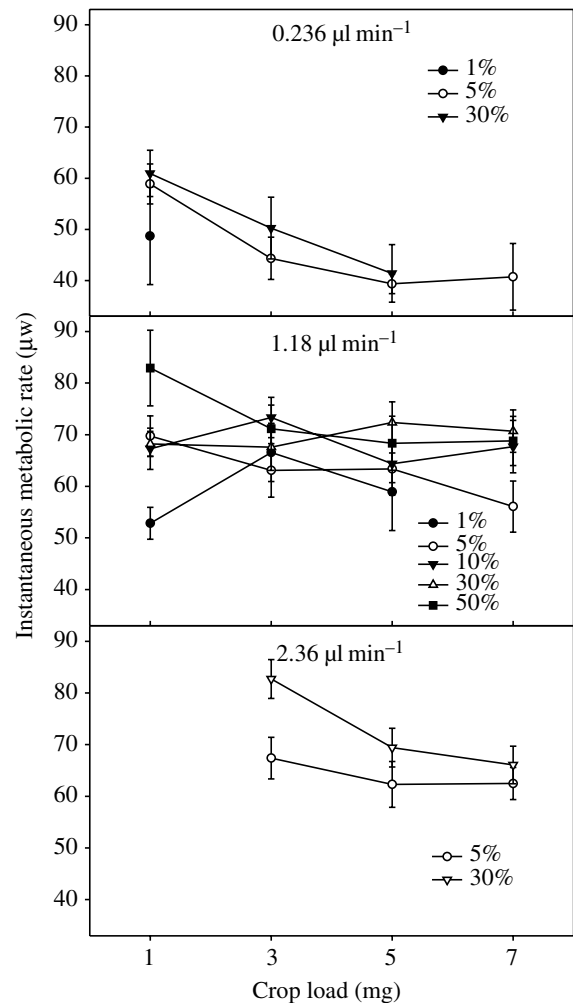

Fig. 5. Instantaneous metabolic rates (μW) as a function of crop load expressed in mass (1, 3, 5 and 7 mg) at three different flow rates (0.236, 1.18 and 2.36 μl min^{-1}). Values are means ± s.e.m. (N=3–17).

forager gained ca. ten times of what it spent. A forager's energy gain–cost ratio significantly increased to a maximum value of ca. 220 times for the highest profitability assayed ($F_{1,123}$=9.630, P<0.005). The positive correlation clearly shows an increase of the individual metabolic rate with the profitability of the exploited nectar source.

Based on the data of costs and gains, it is possible to estimate the maximum distance traveled by a *C. rufipes* forager in a foraging trip with the energy gained during the collection of a nectar load, by using the following simplified model: Assuming no energy (E) loss, then:

$$E_{gain} - E_{spend} = 0 . \quad (3)$$

The maximum distance traveled (D_{max}) with the gained energy will be:

$$E_{gain} - \{GCOT_u(M_{out})/2 + [GCOT_u(M_{out}) + 0.61GCOT_u(M_{load})]/2\} \times D_{max} = 0 . \quad (4)$$

Table 1. *Instantaneous metabolic rates that allowed the comparison among workers having the same crop loads, but collecting at different flow rates or concentrations*

Flow rate (μl min^{-1})	Concentration (%)	Load (mg)			
		1	3	5	7
0.236	1	48.72±9.53 b**			
0.236	5	58.88±3.91 a*	44.33±4.13 a*; b**; c***	39.36±1.92 a*; b**; c*	40.72±6.51 a*; b*; c*; d*
0.236	30	60.94±4.53	50.26±6.03 d**	41.38±5.63	
1.18	1	52.84±3.08 c***	66.57±5.64	58.94±7.51	
1.18	5	69.73±3.90	63.10±5.18 e*	63.38±5.09	56.07±4.95
1.18	10	67.27±3.99	73.33±3.92 b**	64.35±3.64	67.70±5.08 a*
1.18	30	68.21±2.43	67.60±4.51	72.35±3.99 b**	70.70±4.11 b*
1.18	50	82.91±7.32 a*; b**; c***	71.16±4.60 a*	68.35±5.23 a*	68.79±4.74 c*
2.36	5		67.38±4.03	62.31±4.44	62.47±3.10
2.36	30		82.70±3.76 d**; e*; c***	69.43±3.75 c*	66.08±3.63 d*
ANOVA		$F_{7,86}$=4.699, $P<0.001$	$F_{8,104}$=4.666, $P<0.001$	$F_{8,85}$=3.065, $P<0.005$	$F_{6,64}$=2.896, $P<0.02$

The instantaneous metabolic rate (μW) was calculated averaging 45 s of the recording, within which the worker reached either 1, 3, 5 or 7 mg of load during their feeding activity. See Materials and methods for a detailed explanation.

Values are means ± s.e.m. (*N*=3–17). After ANOVA for each load mass *a posteriori* Tukey test was performed. Tukey comparisons were between pair of letters (e.g. a,a or b,b, etc). *$P<0.05$, **$P<0.01$ and ***$P<0.001$.

Thus,

$$D_{max} = E_{gain}/\{GCOT_u(M_{out})/2 + [GCOT_u(M_{out}) + 0.61GCOT_u(M_{load})]/2\} , \quad (5)$$

where the energy gained is a function of the volume crop load and sucrose concentration of the collected nectar, corresponding to 17.1 J mg^{-1} sucrose (Eckert et al., 1990). The energy spent for a round foraging trip (the ant goes unladen and come back to nest loaded) is a function of the mass load and ant mass. *M* is mass and GCOT$_u$ is the gross cost of transport of an unladen worker, which has a value of 264 J kg^{-1} m^{-1} for *C. rufipes* and a cost of load carriage is 61% that of somatic load carriage (Schilman and Roces, 2005).

With Eqn 5, the predicted values of maximum distances traveled are between 0.5 to 9 km, assuming no energy losses, for nectar loads ranging between 1 and 6 mg and nectar concentrations between 20 and 60%, which are values observed in nature (Dreisig, 2000; O'Dowd, 1979) (Fig. 7).
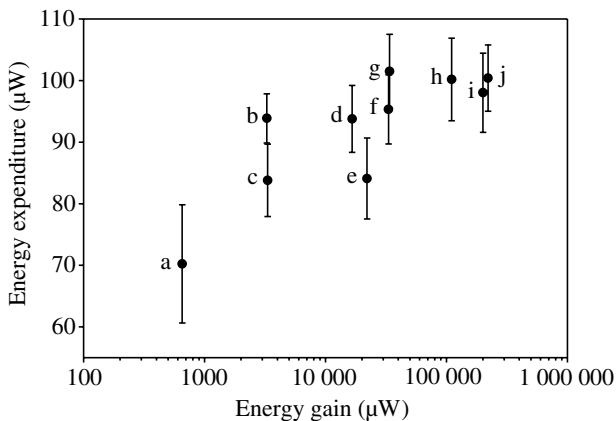
Discussion
Effect of the profitability of the food source on metabolic rates

Although there was a tendency for the metabolic rates of the ants to increase with the concentration of the sucrose solution

Fig. 6. Relation of energy losses and gains expressed in μW for different nectar flow-rates and concentrations. Energy expenditures are measured metabolic rate of ant workers and the energy gain is calculated from the sucrose concentration and flow rate delivery of sugar solution from the artificial feeder. (a) 0.236 μl min^{-1} flow rate and 1% sucrose concentration, (b) 1.18 μl min^{-1} and 1%, (c) 0.236 μl min^{-1} and 5%, (d) 1.18 μl min^{-1} and 5%, (e) 0.236 μl min^{-1} and 30%, (f) 2.36 μl min^{-1} and 5%, (g) 1.18 μl min^{-1} and 10%, (h) 1.18 μl min^{-1} and 30%, (i) 1.18 μl min^{-1} and 50%, and (j) 2.36 μl min^{-1} and 30%. Note the logarithmic scale of the *x*-axis.
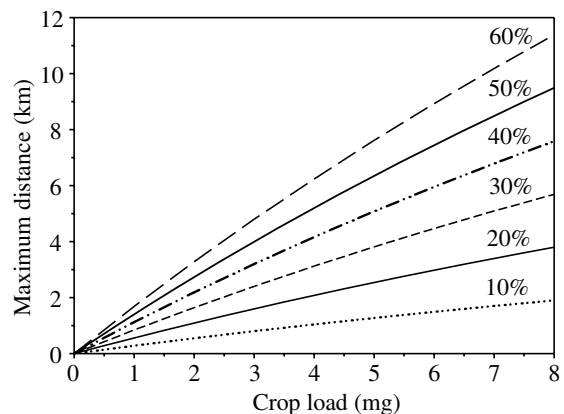

Fig. 7. Relation of the possible maximum distance (km) traveled by a forager with the energy gained in a foraging trip. Energy gained is a function of volume of crop load and concentration of the sugar solution.

Table 2. *Relationship between metabolic rates and final crop load for the different flow rates and sugar concentrations of the food source in visit numbers 1 and 4*

Flow rate (μl min^{-1})	Concentration (%)	Visit	a	b	r^2	P	N
0.236	1	1	78.61	−19.87	0.271	0.290	6
		4	61.12	−5.36	0.008	0.870	6
	5	1	70.33	−3.37	0.085	0.414	10
		4	55.64	−1.84	0.359	0.067	10
	30	1	52.34	−0.31	0.003	0.906	8
		4	48.71	0.25	0.001	0.930	8
1.18	1	1	69.01	−1.69	0.028	0.584	13
		4	68.81	−3.37	0.191	0.136	13
	5	1	86.07	−3.12	0.066	0.321	17
		4	60.70	0.66	0.017	0.614	17
	10	1	87.63	−0.98	0.008	0.773	13
		4	91.20	−1.41	0.065	0.762	13
	30	1	57.02	4.62	0.087	0.286	15
		4	60.28	2.61	0.196	0.099	15
	50	1	72.53	4.50	0.160	0.125	16
		4	76.99	2.49	0.108	0.215	16
2.36	5	1	54.74	2.92	0.062	0.411	13
		4	17.62	5.48	0.333	0.039	13
	30	1	127.22	−3.13	0.155	0.164	14
		4	65.49	1.83	0.063	0.389	14

Data were taken from the last 4 min of the recordings, when there is no more delivery of sugar solution and the ant is walking around the respirometric chamber with the final crop load (for details see Fig. 2 and Materials and methods).

We used the linear regressions ($y=a+bx$) to correlate metabolic rates with loads in *C. rufipes* ant workers. r^2: correlation coefficient, P: probability of error, N: number of tested individuals, y: metabolic rate (μW), x: crop load (mg).

collected, no significant difference was found (Fig. 3C). Considering that the crop loads largely depend on sucrose concentration, the following can be argued. First, differences in crop load do not have a strong effect on the metabolic rate of ants while collecting nectar. Second, the viscosity of a sugar solution from a non-*ad libitum* food source does not affect metabolic rate. This is clearly demonstrated when one compares the results obtained for 10% and 50% sugar solution concentrations. Both metabolic rate values are similar, but the relative viscosities of the solutions differ, being 1.28 cS for the 10% solution and 9.71 cS for the 50% solution (Wolf et al., 1984). Therefore the 50% sugar solution is 7.6 times more viscous than the 10% one. The similarity of these metabolic rates from different solution viscosities is not surprising since the delivered flow rate was much lower than the insect's maximal ingestion rate, which is about 4 μl min^{-1} (Schilman and Roces, 2003). However, we did observe a significant increase in metabolic rate as a function of the sugar solution flow rate (Fig. 4C). Assuming that an ant experiencing a richer food source will increase its activity and metabolism more than an ant experiencing a poorer food source, the results showed in Fig. 3C and Fig. 4C suggest that flow rate is more important than sucrose concentration for the assessment of resource profitability. This conclusion appears unexpected, since the range of food source richness used (measured as energy content) was larger for the sucrose concentrations than for the flow rates. However, it is suggested that in nature, the amount of nectar found at a source may be a more reliable measure of its richness, as it depends on both the delivered nectar flow and the time elapsed since the last visit.

The increases in metabolic rates with increasing flow rates of sugar solution are unlikely to be a result of an increased activity of the pharyngeal muscles directly involved in fluid feeding, because they are relatively small (Paul et al., 2002), and because there was no increase in metabolic rate between the nectar flows of 1.18 and 2.36 μl min^{-1} (Fig. 4C), for which the ingestion rate has to be varied by a factor of 2. Differences in metabolic rates with nectar flow could not be explained by intrinsic differences among ants in different groups, because no significant differences were detected among experimental groups for the first 4 min of the first visit of the forager ($F_{8,117}=1.269$, NS, one-way ANOVA).

In addition, differences could not be the result of CO_2 dissolved in the nectar and released in the chamber, because control measurements without ants did not show an increase in the CO_2 with nectar delivery. Such a potential experimental artifact should be particularly pronounced in the control groups for two reasons. First, because the nectar accumulated over time, while in the experimental groups the ant immediately collected it. Second, because the measuring times during nectar delivery on control groups were the maximum times measured on the experimental groups, with most of the ants assayed showing

shorter feeding times. However, we found no evidence of CO_2 released from the nectar, with the highest average variation of CO_2 over time being less than 2% of the CO_2 emitted by an ant. The increase of metabolic rates with nectar flow could be the result of an increased activity of the ants. While feeding, ants were observed to perform spontaneous interruptions, as previously described (Schilman and Roces, 2003), briefly running around the source before continuing feeding. However, since these activity bursts were not quantified, the question of how a higher nectar flow increased the ant's metabolic rate remains open. Although a tempting causal explanation for this observed increase could be the load itself, we have to rule out this possibility because our results showed no dependence of metabolic rate on crop load (Fig. 5 and Table 2). In other words, ants collecting nectar at a higher flow rate have a higher metabolic rate compared to ants collecting at lower flows, even when they attain the same crop load.

We cannot exclude the possibility of an increased metabolic rate resulting from an increase in the ant's activity as a result of an enhanced feeding motivation, which is expected to be higher for higher food-source profitabilities. In a previous study, *C. rufipes* workers that previously experienced high nectar flow rates showed a higher activity, in particular a higher rate of drinking attempts at an experimentally depleted patch, than workers that experienced a low flow rate (Schilman and Roces, 2003). In leaf-cutting ants, *Acromyrmex lundi*, foragers were observed to increase their running speed when recruited to a high-quality food source, independent of the load carried (Roces and Núñez, 1993). The same was observed in unloaded leaf-cutting ant workers on their first way to a newly discovered source: they ran at a faster pace, the higher the quality of the food found by the scout ants. The information about food quality that caused this increase in speed was transmitted through recruitment signals (Roces, 1993). Previous studies in honeybees also demonstrated an increased of metabolic rate with increasing sucrose flow rate in free-flying foraging bees, when controlling for load mass (Balderrama et al., 1992; Moffatt, 2000), and also in non-flying foraging bees (Moffatt and Núñez, 1997). Here it is important to note that although honeybees are also nectar-collecting social insects, they have the ability to increase their metabolic rates *via* the activation of the flight muscles and the associated heat production that increases their thoracic temperature.

It is important to mention that the richness of the food source not only influences the metabolic rate of *Camponotus rufipes* foragers but also changes their individual trail-laying behavior, leading to an increase in trail-laying responses with increasing sucrose concentration (P.E.S. and F.R., unpublished data), which may cause increased foraging rates at the colony level.

Activity and catabolic flux rates

As might be expected for an unrestrained ant worker in a novel environment, workers were active throughout the recordings, except for moments while feeding. Thus each ant group collecting the different flow rates and sucrose solutions showed a catabolic flux rate higher than that predicted on the basis of body mass for inactive insects (Lighton et al., 2001). For example, Lighton et al.'s equation [(Lighton et al., 2001): $SMR=973M^{0.856}$, where the standard metabolic rate, SMR, is in μW and the body mass M in g] predicts an SMR of 26.72 μW at 25°C for an ant of 15 mg live body mass. In our study, the mean metabolic rate measured in 6 individual ant workers (mean body mass=14.97 mg) that collected at a flow rate of 0.236 $\mu l\ min^{-1}$ and 1% sugar solution concentration at 25°C was 0.793 $\mu l\ CO_2\ h^{-1}\ mg^{-1}$ of live body mass, which is equivalent to 48.54 μW. Our measurement of metabolic rate was almost twofold higher than previous measurements for caged ants of the same species, i.e. 0.43 $\mu l\ O_2\ h^{-1}\ mg^{-1}$ (Takahashi-Del-Bianco et al., 1998), and also than predicted values from the allometric equation (Lighton et al., 2001). However, allometric equations of SMR were usually based on measurements on decapitated insects. In an unidentified *Camponotus* ant species (mass about 12 mg), a 1.7-fold increase of metabolic power was found when comparing measurements between intact and decapitated ants (Lipp et al., 2005). Thus, this could be an additional explanation for the difference between the measured and the calculated values of SMR, besides the potential effects of locomotion.

Foraging energetics in ants

Energetic measurements of locomotion and load carriage in a wide variety of ant species showed similar low costs, suggesting that natural selection has favored efficient load carriage in ants. These low costs favor a positive gain–cost ratio or energy efficiency in all cases analyzed (e.g. Baroni-Urbani and Nielsen, 1990; Fewell, 1988; Fewell et al., 1996; Weier and Feener, Jr, 1995). Because of such low energy expenditure in foraging ants, the energetic content of the food plays a main role in the outcome of any analysis of energetic efficiency. Consequently, gain–cost ratios varied from 4 for nectar-collectors (Fewell et al., 1996) to 1000 for harvester ants (Fewell, 1988). Comparisons of foraging energetics in *Pogonomyrmex maricopa*, which forages individually, and *P. rugosus*, which employs a trunk-trail foraging system, showed an average energy gain–cost ratio of more than 100 for both species (Weier and Feener, Jr, 1995). This study also showed that for *Pogonomyrmex maricopa* and *P. rugosus*, the estimated energy intake on successful foraging trips was always greater than energy expenditure in the field (Weier and Feener, Jr, 1995). Similarly, our results indicate positive gain-cost ratios, even with the poorest food source assayed (Fig. 6).

On the one hand, measuring energetic costs of foraging in the laboratory with a well controlled environment makes it possible to detect subtle differences, such as the modulation of the metabolic rate by the sucrose flow rate (Fig. 4C). On the other hand, laboratory experiments have the disadvantage of giving rise to possible artifacts in the results. However, a recent field-data validation of laboratory measurements on ant locomotion (Lighton and Duncan, 2002) allows for the extrapolation of our energetic measurements in controlled laboratory conditions to a model of ant's energetic foraging in the field.

The results presented in this study, together with a recent publication on locomotion energetics in the same *Camponotus* species (Schilman and Roces, 2005), allowed us to develop a simple model of foraging energetics for the nectar-feeding ant, *C. rufipes*. This model shows that single foraging workers of *C. rufipes* have an autonomy of about 10 km of maximum distance traveled with the energy collected in a foraging trip from a high-quality food source (Fig. 7). A similar distance was calculated for the harvesting ant, *Messor capitatus*, from the energetic content of wheat seeds (Baroni-Urbani and Nielsen, 1990). However, we have to be cautious in taking this oversimplified model as an indirect measure of colony fitness, because only a proportion of the workers in the colony are foragers and the energy gathered by foragers should maintain all colony members, even those workers performing inside-nest tasks. [Also see discussion elsewhere (Lighton and Duncan, 2002).] Future research under field conditions will help make this model more accurate.

Partial crop loads: time vs energy saving

In foraging honeybees, it was hypothesized that a forager returns to its hive with partial crop loads in order to maximize its efficiency (ratio of gain to cost) (Kacelnik et al., 1986; Schmid-Hempel et al., 1985). This 'energetic' hypothesis found support in some studies (e.g. Wolf et al., 1989), but not in others (Balderrama et al., 1992; Moffatt, 2000), and also Feuerbacher et al. (Feuerbacher et al., 2003) to some extent. An alternative explanation is that returning earlier with partial crop loads increases the probability of information exchange at the colony, and thus favors colony efficiency, as first suggested by Núñez (Núñez, 1979; Núñez, 1982). This 'informational' hypothesis was also investigated in other social insects, i.e. leaf-cutting ants (Roces, 2002; Roces and Hölldobler, 1994; Roces and Núñez, 1993), and the nectar-feeding ant used in this study (Schilman and Roces, 2003). The results on load-size selection for the three different systems (i.e. honeybee, leaf-cutting and nectar-feeding ants) support the informational hypothesis, even though the species considered largely differ in terms of their energetic expenditures for locomotion and food gathering. For example, nectar intake by honeybees is a low-cost activity, while flying to and from the hive and from one flower patch to another is a high-cost activity (Nachtigall et al., 1989). For leaf-cutting ants, cutting a leaf fragment is highly expensive (Roces and Lighton, 1995), while carrying it back to the nest is much less costly (Lighton et al., 1987). Finally, for *C. rufipes*, both collection and carrying are low cost activities (the present study) (Schilman and Roces, 2005). The 'informational' hypothesis seems robust because it helps to explain the results found in three diverse systems, i.e. three social insect species with different energetic investments during foraging. In addition, while the 'energetic' hypothesis clearly focuses on the individual level because foraging rules are considered to increase the efficiency of the individual forager, the 'informational' hypothesis emphasizes the colony level, i.e. strategies that increase the benefit to the colony as a whole, even at expenses of reduced performance at the individual (forager) level.

Finally, the calculations of losses and gains during nectar collection, together with the fact that the cost of load carrying is about 40% cheaper than carrying its body mass (Schilman and Roces, 2005), support the hypothesis that saving time (with the potential increase in colony-wide energy intake *via* social recruitment) is more important than saving energy (or increasing individual forager efficiency) when workers of the nectar-feeding ant *C. rufipes* decide to stop drinking and come back to the nest with partially filled crops.

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